CUTICLE ULTRASTRUCTURE OF A JURASSIC CRUSTACEAN (*ERYMA STRICKLANDI*)

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ABSTRACT. The cuticle of well-preserved pieces of the fossil lobster *Eryma stricklandi* from the Oxford Clay yields information on its ultrastructure when compared with cuticle of the closely related living crayfish, *Astacus fluviatilis*. In both species the pore canals which traverse the laminated layers of the cuticle are large enough to be analysed in the light microscope. In sections cut almost tangential to the surface both species show the pore canals crescentic in section and with the crescents arranged to form a repeating pattern of rows of concentric parabolae. From living material previously investigated by electron microscopy and from model building, it is clear that this pattern arises from oblique sections of fields of pore canals which are tubes with elliptical cross-section and which twist regularly and in unison about their axes. This twisting is caused by the architecture of the surrounding chitin microfibrils which are arranged in parallel layers. Each layer is set at a slight angle to the preceding one so as to form a progressively rotating structure known as a helicoid. We deduce that the cuticle in *Eryma* is also helicoidal, and that this system evolved in arthropod cuticle at least as early as the Jurassic.

PUBLISHED photographs of sections of fossil arthropod cuticles do not permit any deductions as to their ultrastructure, beyond saying that they are laminated (e.g. the trilobites, *Phacops accipitrinus* in Rome 1936, and various trinucleids in Størmer 1930). Cuticles of Silurian Crustacea show laminae and pore canals (Rolfe 1962). By analysis of the pore canals in living material, we are now able to deduce the architecture of the surrounding chitin microfibrils (Neville, Thomas, and Zelazny 1969), and these results have been confirmed in the electron microscope (Neville and Luke 1969*a*, *b*). In this paper we use this method to gain information about ultrastructure in the cuticle of a fossil lobster (*Eryma stricklandi*) from the Oxford Clay. We have made use of the very large pore canals typically found in Crustacea, permitting their analysis in the light microscope, and have been fortunate in finding fossil material in which the matrix through which the pore canals run is remarkably well preserved. This is probably aided by the marked insolubility of most cuticular components. For comparison with the cuticle of *Eryma* we have used the living freshwater crayfish, *Astacus fluviatilis*. Both species are classified in the infra-order Astacidea Latreille 1803.

Material and Methods. Fragments of the exoskeleton of *Eryma stricklandi* were collected from the Oxford Clay (Jurassic) from a gravel pit on Standlake Common, near Witney, Oxfordshire. The region worked on was the cuticle of the propodite segment of a cheliped limb (Pl. 30, fig. 1). Results were compared with the cuticle of the same region from a living freshwater crayfish (*Astacus fluviatilis*).

Fossil cuticle was either chipped off the infilling matrix of calcite and iron pyrites or sectioned *in situ*. Some pieces were ground flat on one face, deliberately made slightly oblique to the cuticle surface to reveal the patterns in the photographs. The flat faces were glued to a glass microscope slide with Lakeside 70 glue and ground by hand using fine grade corundum powder until thin enough sections were obtained. Other pieces were sectioned vertically to the cuticle surface.

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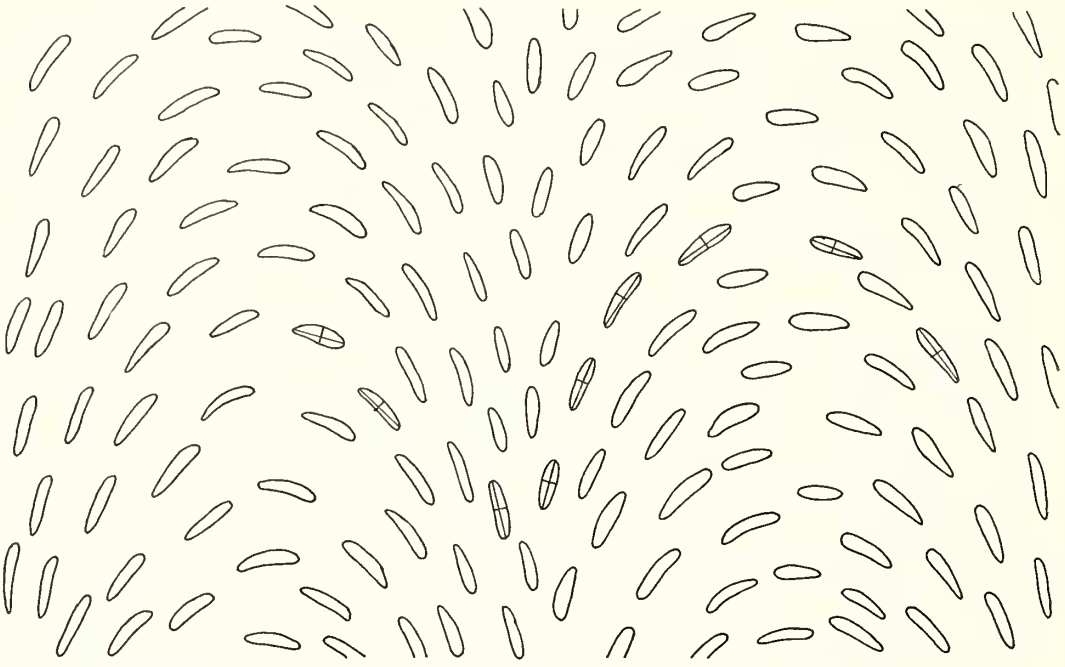
For comparison, decalcified pieces of *Astacus* cuticle were softened in 70% ethanol and sections cut by hand with fresh razor blades at a glancing angle to the surface. Sections were examined in Zeiss polarizing and phase-contrast microscopes.

Results. Sections cut vertical to the cuticle surface are compared for *Astacus* (Pl. 31, fig. 1) and the fossil *Eryma* (Pl. 31, fig. 2). The wide lamellation of the endocuticle (deposited after the moult) is clear in both cases, but the finer lamellation in the exocuticle (deposited before the moult) is visible only in *Astacus*.

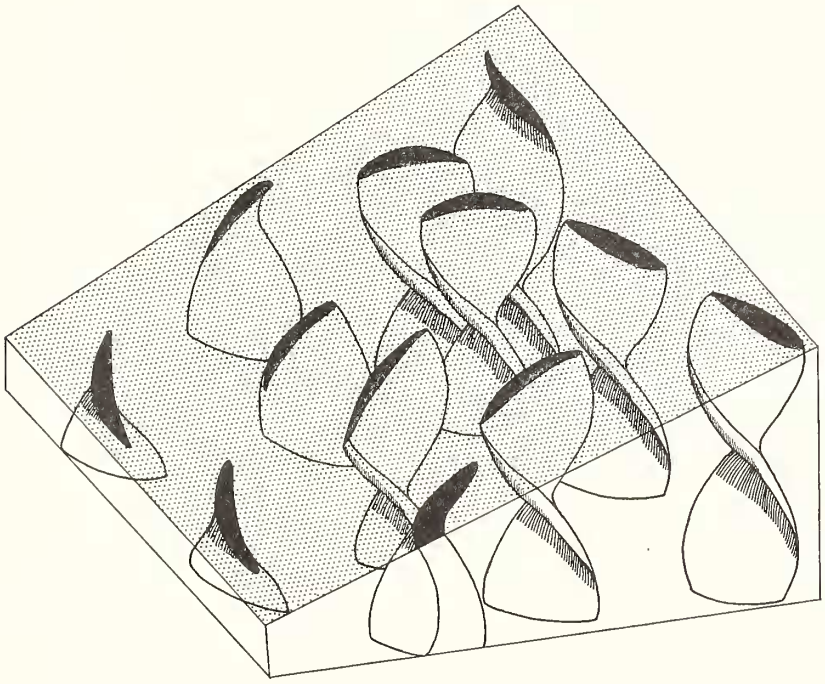


TEXT-FIG. 1. Diagram of the parabolic pattern formed by obliquely sectioning a field of twisted ribbon pore canals, twisting in phase as described in the text. The pore canals in *Eryma stricklandi* are infilled with calcite. Optical indicatrices are shown in some of the canals.

Pore canals, which in Crustacea are responsible for transporting the calcium carbonate used in post-moult stiffening from the underlying epidermal cells (Travis 1963), appear as lines running vertically to the cuticle surface and hence also to the lamellae. In Plate 30, fig. 2, of *Eryma*, the pore canals are especially large and clear between crossed polaroids, being filled with birefringent calcite (negative with respect to pore canal length). It is significant that the pore canals appear sinuous and that the curves are in register with the lamellae.

The most informative sections are those which are cut *almost* tangentially to the cuticle surface. Both in *Astacus* endocuticle (Pl. 32, fig. 1) and *Eryma* endocuticle (Pl. 32, fig. 2), the obliquely sectioned pore canals form parabolic patterns. Each canal has a crescentic cross-section and in the case of the calcite-filled fossil pore canals the crescents are positively birefringent along their greatest dimension (text-fig. 1).

Discussion. Parabolic patterns like those in Plate 32, figs. 1 and 2, were first drawn for lobster (*Homarus*) cuticle by Drach (1939), but an interpretation was not available until recently (Neville, Thomas, and Zelazny 1969). We deduced from model building and sectioning that each pore canal consists of a tube which is elliptical in cross-section, and which is regularly twisted about its longitudinal axis so as to form a twisted ribbon. Such a twisted ribbon has since been photographed in spider cuticle (Barth 1970). A whole field of pore canals twist in register with each other. Sections cut obliquely to



TEXT-FIG. 2. Diagram showing the origin of a parabolic pattern (in black) of pore canals, arising on an oblique plane of section (stippled), cut through a field of canals which twist in unison. Reconstructed from an electron micrograph of *Astacus* cuticle.

the pore canal axes then show parabolic patterns of the type drawn in text-fig. 1, and as seen in Plate 32, figs. 1 and 2. The origin of this pattern is illustrated in text-fig. 2.

Such parabolic patterns of pore canals give information about the ultrastructure of the surrounding cuticle. Arthropod cuticles consists of chitin microfibrils (diameter 50 Å) embedded in a protein matrix to form a fibreglass-like system (Neville 1970). The microfibrils are oriented in parallel sheets with the direction of orientation in successive sheets progressively rotating to form a helicoidal stack (Bouligand 1965, Neville and Luke 1969*b*). It is this rotation which causes the pore canals to twist at the same pitch. Consequently, we deduce from Plate 32, fig. 2, that the cuticle in *Eryma stricklandi* was also helicoidal. This also explains the lamellae seen in vertical sections with polarized light (Pl. 30, fig. 2, and Pl. 31, fig. 2) since birefringence due to the microfibrils will be alternately maximal and minimal for each 90° rotation of the helicoid (i.e. microfibrils

lying in the plane of section or perpendicular to it respectively). Also, the twisted ribbon structure for pore canals explains the sinusoidal appearance in register with the lamellae seen in Plate 30, fig. 2.

It seems as if the helicoidal type of architecture, which we have seen in all present day arthropod cuticles examined so far, evolved at least as early as the Jurassic period. We are eager to pursue this in earlier fossil arthropods, especially in suitably preserved Trilobites.

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EXPLANATION OF PLATE 30

Fig. 1. Propodite segment of cheliped of *Eryma stricklandi,* ×11; Oxford Clay.

Fig. 2. Photomicrograph of section cut vertical to surface of cuticle of *Eryma stricklandi* between crossed polaroids showing lamellation and pore canals with sinuous shape (arrowed) in phase with the lamellae, ×500.

EXPLANATION OF PLATE 31

Fig. 1. Photomicrograph of section cut vertical to surface of cuticle of living *Astacus fluviatilis* viewed between crossed polaroids, ×300.

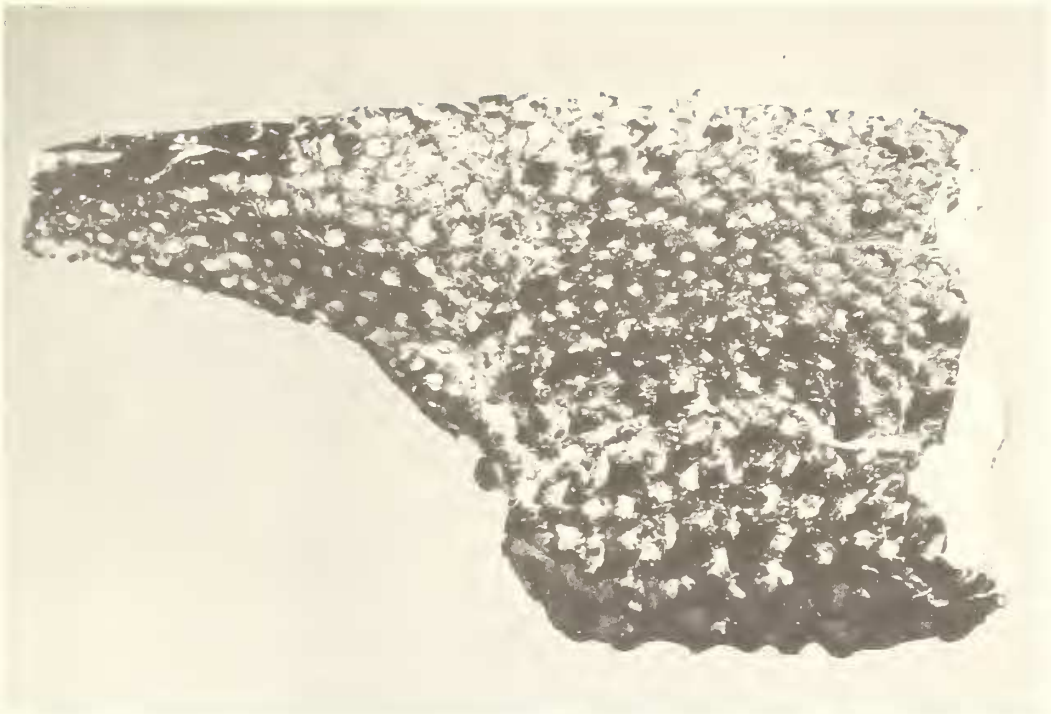
Fig. 2. Photomicrograph of section cut vertical to surface of cuticle of *Eryma stricklandi* viewed between crossed polaroids, ×800.

Exo, exocuticle; *endo,* endocuticle.

EXPLANATION OF PLATE 32

Fig. 1. Photomicrograph of section cut almost tangential to surface of cuticle of living *Astacus fluviatilis,* viewed in phase contrast; the pore canal sections, seen here in the endocuticle, form a parabolic pattern, ×2500.

Fig. 2. Photomicrograph of section cut almost tangential to surface of fossil cuticle of *Eryma stricklandi,* viewed between crossed polaroids and compensated by a first order red plate; the pore canals again form a parabolic pattern, ×1000.



1

2

NEVILLE and BERG, Jurassic crustacean cuticle